SHRUB FACILITATION OF COAST LIVE OAK ESTABLISHMENT IN CENTRAL CALIFORNIA

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ABSTRACT

Seedlings of *Quercus agrifolia* were found to be strongly associated with shrubs at two sites in central California. Although shrub cover occupied only 30% of the total cover, over 80% of all *Q. agrifolia* seedlings were found under shrub canopies. Although one site was grazed by livestock and the other was not, in both sites seedlings under shrubs were less browsed than seedlings in the open grassland. In field experiments where seedlings were grown with and without shrub cover, survivorship after two years in the open was 0, whereas 31% of seedlings survived under shrubs (18% of the experimental shrubs had living seedlings under their canopies). Seedling survival was not the same under all shrub species. Shoot mortality in these experiments attributed to water or temperature stress was 17% under shrubs and 63% in the open. These results indicate that *Q. agrifolia* may have a "nurse plant" interaction with some species of shrubs.

Recruitment of young *Quercus agrifolia* Nee (coastal live oak), is too low to maintain the existing adult populations in much of its range (Muick and Bartolome 1987) and the preservation of this woodland has become a major conservation issue in California, USA. Although the factors that limit regeneration of other oak species in the state are complex, they include drought stress and seedling predation from deer, gophers and livestock (Griffin 1971, 1976; Borchert et al. 1989). The causes of low regeneration of *Q. agrifolia* have not been studied, but they are likely to be similar to those reported for other species.

Quercus agrifolia is an evergreen tree, 10 to 20 m tall, and is endemic to California, USA and northern Baja California, Mexico (Munz 1959). It is widely distributed throughout the central and southern coastal ranges of California and is often adjacent to shrub vegetation or intermixed with shrubs (Sawyer et al. 1977). Acorns mature and drop to the ground and/or are dispersed by vertebrates in autumn and germination occurs in late autumn or early winter. The climate in which the species occurs is mediterranean, with precipitation occurring primarily between September and April.

Muick and Bartolome (1987) reported that seedlings and saplings of *Q. agrifolia* were uncommon in many of their study sites. In

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MADROÑO, Vol. 38, No. 3, pp. 158–169, 1991

preliminary surveys we also found that young *Q. agrifolia* were uncommon, but that seedlings and saplings appeared to be associated with shrub cover. This observation is consistent with the following hypotheses: 1) acorns are not randomly dispersed between open grassland and shrub cover; 2) germination rates are not the same in these microhabitats; and/or 3) seedling survival is restricted to certain microhabitats. The latter two hypotheses have been investigated in other plant associations and have been included in the general phenomenon of "nurse plant" interactions in which established plants ameliorate climatic extremes and /or provide refuge from predators for seedlings of other plant species. Such associations have been previously reported for a wide range of desert taxa and habitats (Steenbergh and Lowe 1977; Everett et al. 1986; Franco and Nobel 1989; McAuliffe 1988), but not for oaks or other species in California woodlands.

To test the hypothesis that oak tree seedling recruitment is dependent upon a nurse plant association with established shrubs, we documented the natural distribution and condition of *Q. agrifolia* seedlings and saplings relative to shrub cover in two sites, each with approximately equal cover of mixed oak savanna and chaparral. We then followed the survivorship of seedlings planted from acorns both in the open and under shrubs at a third site, and documented the probable causes of mortality of these seedlings over two years.

STUDY SITES

Natural distributions of seedlings in the field were measured at two sites in the Santa Ynez Valley in northern Santa Barbara County. The first site was a mixed oak woodland at Cachuma State Park (200 m elevation, 34°35′N, 119°59′W) where stands of *Q. agrifolia* and *Q. lobata* Nee (valley oak) were scattered throughout annual grassland and adjacent to coastal scrub dominated by *Salvia leucophylla* E. Greene (purple sage) and *Artemisia californica* Less. (California sagebrush). The site had been free from livestock grazing for over 10 years, but native herbivores such as mule deer (*Odocoileus hemionus*) and pocket gophers (*Thomomys bottae*) were common. The second site was located at Sedgwick Ranch, in the Santa Ynez Mountains (350 m elevation, 34°41′N, 120°2′W). Here *Q. agrifolia* was mixed with *Q. lobata* and *Q. douglasii* Hook. & Arn. (blue oak) and occured adjacent to coastal scrub dominated by *S. leucophylla* and *A. californica*. This site was grazed by livestock as well as native herbivores.

An experiment to test the hypothesis that shrubs facilitate establishment of oak seedlings was set up at a third site in northern Santa Barbara County in conjunction with a revegetation project. This site was located approximately 8 km W of the other two sites at the base of the Purisima Hills (200 m elevation, 34°32′N, 120°27′W). The experiment was established in a oil pipeline right-of-way that formerly had supported both *Q. agrifolia* and a variety of shrub species. Shrubs, primarily *A. californica, Ericameria ericoides* Jepson, *Mimulus aurantiacus* Curtis, and *Lupinus chamissonis* Eschsch., had reestablished on the right-of-way by both artificial and natural seeding during the two years between the completion of the pipeline and the beginning of the experiment. Soil at this site was uniformly medium sand (Davis et al. 1988) underlain by marine sedimentary rocks and gravels which are covered with Orcutt sandstone (Dibblee 1950). The section of right-of-way that we used followed gently rolling topography with slope steepness ranging from 0 to 3%, and slope aspects facing either E or W. Rainfall averaged 36 cm annually. Livestock were excluded from this site but natural predators including mule deer and pocket gophers were abundant.

METHODS

Natural seedling distribution. We searched for naturally occurring seedlings in ten 20 × 20 m plots at Cachuma and eight 20 × 20 m plots at Sedgwick Ranch that had been randomly located in the woodland-shrubland ecotone. We recorded the number of oak seedlings, vegetative cover type with which seedlings were associated (seedlings under shrub and tree canopies were recorded as associated with the cover type of the shrub species), average diameter of each shrub canopy associated with an oak seedling, the percentage of leaves that were brown on each seedling, and the percentage of leaves that had been browsed in each plot. All field distribution patterns were sampled in the fall of 1987, before the current crop of acorns had germinated. Thus, only seedlings that had germinated in 1986 or before were recorded. We use the term "seedling" for continuity, however, many were several years old.

Experimental seedling establishment. In November 1987, viable acorns that had been collected at the Purisima Hills site were planted in 100 plots in the following experimental design. Each plot was centered on a randomly chosen shrub, regardless of species, which was permanently tagged. The species of shrubs that were used were *A. californica* (23 shrubs), *E. ericoides* (49 shrubs), *M. aurantiacus* (19 shrubs), and *L. chamissonis* (9 shrubs). These shrubs had regenerated after the completion of construction, two years prior to our experiment. Shrubs were from 30 to 55 cm tall, and 35 to 50 cm in diameter. Four acorns were buried 2 cm deep under each central shrub, approximately 20 cm apart, one at each cardinal compass point under the shrubs. Four acorns were also planted in the open, one at each cardinal compass point 1 m from the edge of the

TABLE 1. DISTRIBUTION OF *QUERCUS AGRIFOLIA* SEEDLINGS WITH RESPECT TO VEGETATION COVER TYPE. Chi-square statistics are for goodness-of-fit tests for numbers of seedlings associated with a given cover type.

Study area	Cover type	Relative frequency	Number of associated *Quercus agrifolia* seedlings Obs.	Exp.
Cachuma	Open grassland	0.605	6	126
	Quercus agrifolia	0.038	35	8
	Artemisia californica	0.193	73	40
	Salvia leucophylla	0.162	94	34
		n = 208 seedlings $\chi^2 = 338.5$, df = 3, $p < 0.001$		
Sedgwick	Open grassland	0.581	0	28
	Quercus agrifolia	0.118	7	6
	Artemisia californica	0.107	11	6
	Salvia leucophylla	0.165	31	8
		n = 49 seedlings $\chi^2 = 98.5$, df = 3, $p < 0.001$		

shrub canopies. Thus, the total number of acorns planted was 400 under shrubs (100 shrubs) and 400 in the open.

Shoot emergence was first recorded in March 1988 and survivorship of shoots was recorded in July and September 1988, January 1989, and February 1990. We recorded the presence of dead, desiccated shoots and missing shoots in order to estimate mortality due environmental stress and that due to herbivory. Survivorship was analyzed by plot to avoid psuedoreplicaton, and also by individual seedlings. Statistics were conducted with Systat (Wilkinson 1988).

RESULTS

Natural seedling distributions. Numbers of naturally established oak seedlings were much higher under shrubs than in the open grassland in both of the surveyed study sites. At the Cachuma site, the most common shrubs, *S. leucophylla* and *A. californica,* covered 36% of the total study area but 80% of all *Q. agrifolia* seedlings were found under these two species (Table 1). Only 3% of the seedlings were found in the open grassland, yet this was the predominant cover class at the site. At Sedgwick, the site with livestock, the same shrub species occupied 27% of the total study area but 86% of all oak seedlings were found under them, and no seedlings were found in the open grassland (Table 1). In both of the study sites approximately 15% of the seedlings were located under adult *Q. agrifolia* trees and with no shrub cover, but at the Cachuma site the number of oak seedlings found under adult oak canopies was four times that

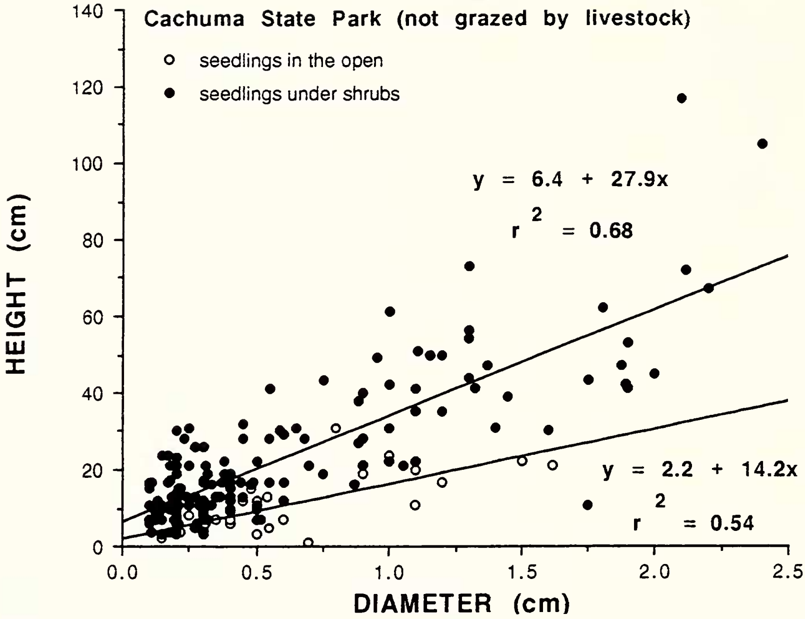

FIG. 1. Regression of *Quercus agrifolia* seedling diameter (2 cm above soil surface) and seedling height at Cachuma State Park.

expected on the basis of the relative frequency of this cover type (Table 1). At the Cachuma site the total density of oak seedlings was 5.2 ± 6.0 (SD) per 100 m^2, whereas at the Sedgwick site total seedling density was 1.5 ± 1.8 per 100 m^2. Seedling distributions were highly clumped, as indicated by variance to mean ratios of 49.4 and 7.0 for the Cachuma and Sedgwick Sites respectively (see Whittaker 1975). There was no difference in the percent of seedling foliage that was brown between seedlings under shrubs and seedlings in the open in either site, but browsing intensity was substantially higher in the open grassland and under adult *Q. agrifolia* canopies than under shrubs (Table 2). Regression equations between the height and diameter of seedlings (2 cm above the soil surface) showed that seedlings under shrubs tended to be taller than seedlings of similar diameters in the open grassland (Fig. 1), and in many cases the seedlings had overtopped the shrubs in which they grew.

Experimental seedling establishment. Although acorn germination occurs shortly after the first heavy rains, shoots are often not visible until the late winter. In March 1988, five months after planting, we located 117 seedlings under experimental shrubs (29% of the planted acorns) and 69 seedlings in the open near the shrubs (17% of the

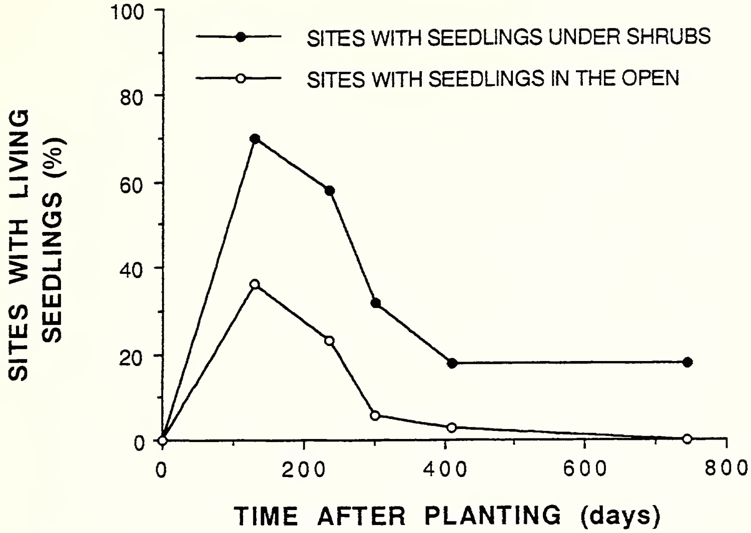

FIG. 2. Percentage of plots with surviving *Quercus agrifolia* seedlings under shrubs, and percentage of plots with surviving *Q. agrifolia* seedlings in the open in the Purisima Hills. Acorns were planted in November 1987.

planted acorns). Within two years all seedlings in the open had died or disappeared, whereas 18% of the plots had living seedlings under shrubs (Fig. 2) and 36/117 (31%) of the seedlings under shrubs were still alive (Fig. 3). Some resprouting of "dead" seedlings occurred during the experiment as can be noted in the slight increase in survivorship under shrubs between January 1989 and February 1990.

TABLE 2. CHARACTERISTICS OF NATURALLY ESTABLISHED *QUERCUS AGRIFOLIA* SEEDLINGS UNDER SHRUBS AND IN THE OPEN AT CACHUMA STATE PARK. Diameter was recorded 2 cm above the soil surface. x̄ ± SD = mean plus or minus one standard deviation. Shared letters indicate means that are not statistically different (Tukey HSD, $p < 0.05$).

Cover type	Diameter (cm) x̄ ± SD		Height (cm) x̄ ± SD		Browsed (%) x̄ ± SD		Brown (%) x̄ ± SD	
A. californica (n = 71)	0.59^a	0.51	21.3^a	14.2	7.7^a	14.0	14.1^a	20.9
S. leucophylla (n = 93)	0.51^a	0.50	20.4^a	19.4	8.7^a	14.7	12.6^a	15.3
Quercus agrifolia (n = 34)	0.46^a	0.25	8.7^b	5.2	52.9^b	32.2	15.6^a	18.0
Open grassland (n = 6)	0.90^a	0.61	13.8^b	8.2	50.0^b	35.9	20.0^a	12.6

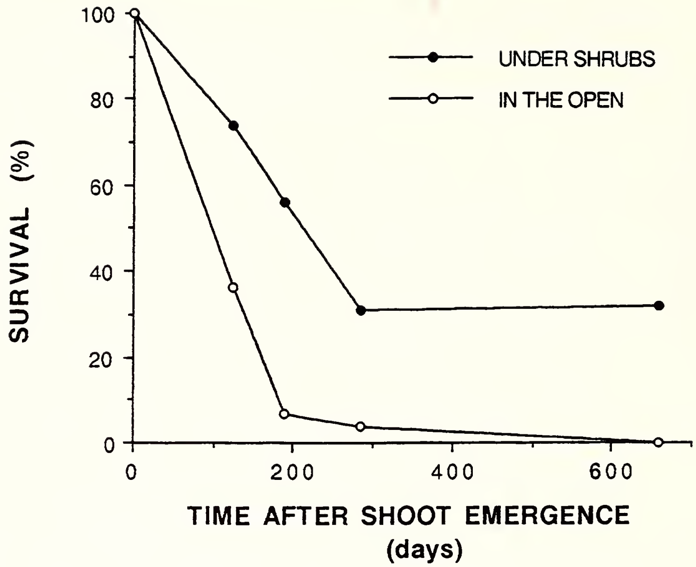

FIG. 3. Survivorship of *Quercus agrifolia* seedlings under shrubs and in the open in the Purisima Hills. Survival is presented as the percent of the original cohort remaining at each date. Shoots were first counted in March 1988.

During the first six months after emergence the rate of mortality was 64/69 (93%) of the seedlings in the open in comparison to 50/117 (43% under shrubs (Fig. 3). Of the 81 seedlings that died under shrubs, 14 (17%) dried in place and 67 (83%) disappeared (shoots were missing). Of the 69 seedlings that died in the open, 43 (62%) dried in place and 26 (38%) disappeared. Herbivore species may have differed under shrubs and in the open. In the open, most shoots disappeared with no evidence of soil disturbance and were probably eaten by deer, based on the abundance of scat and tracks. Shoot disappearance under shrubs was usually associated with conspicuous gopher tunneling.

Not all species of shrubs facilitated oak establishment. In plots with *E. ericoides* as the central shrub, 14/49 (29%) plots had living seedlings under shrub cover after two years. In comparison, 4/23 (17%) sites with *A. californica,* 1/19 (5%) sites with *M. aurantiacus* and 0/9 sites with *L. chamissonis* as central shrubs had living oak seedlings under the shrub canopies after two years. Total seedling survival was 24/56 (43%) under *E. ericoides,* 11/32 (34%) under *A. californica,* 1/22 (5%) sites under *M. aurantiacus,* and 0/7 under *L. chamissonis.* Oak seedling survival did not differ significantly between *E. ericoides* and *A. californica* whether analyzed by plot (χ^2

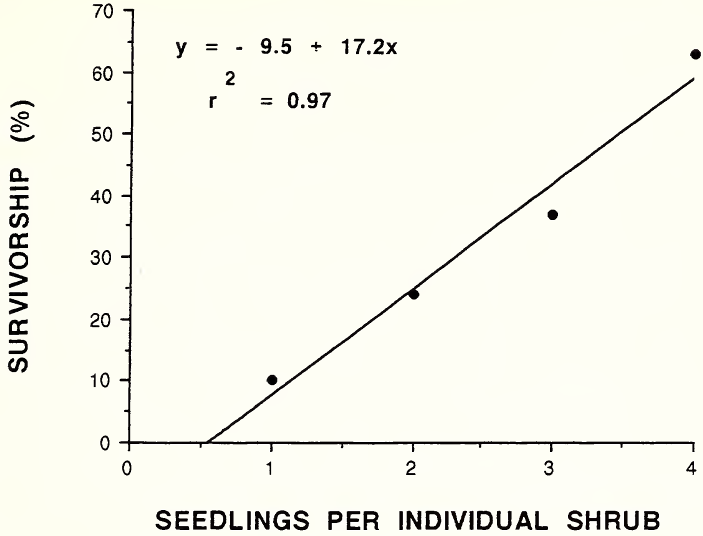

FIG. 4. Regression of the number of shoots emerging under individual shrubs in March 1988 and survivorship in these categories in February 1990 at Purisima Hills.

= 0.98, $p > 0.5$) or by total number of seedlings ($\chi^2 = 0.42$, $p > 0.4$).

Survivorship was inversely correlated with the number of seedlings that emerged under an individual shrub (Fig. 4). Of the seedlings that emerged in groups of four, 63% survived for the entire experiment, whereas only 10% of the seedlings that emerged alone under shrubs survived.

DISCUSSION

Our data strongly indicate that some shrubs may act as nurse plants for *Q. agrifolia* seedlings. Distributions of naturally established seedlings were highly associated with shrubs, and seedlings under shrubs were less browsed than seedlings in the open. Our field experiments showed that oak seedling survivorship under shrubs was significantly higher than survivorship in the open only 1 m from the shrubs. At the time of our first sampling more seedlings were present under shrubs than in the open, which suggests that either germination conditions were more favorable under shrubs, acorn predation was lower under shrubs, or that our first sampling date missed high rates of predation in the open soon after emergence.

The number of seedlings under adult *Q. agrifolia* canopies site was higher than expected on the basis of cover frequency at the Cachuma site and as high as expected at the Sedgwick site (Table

1). This suggests that *Quercus agrifolia* seedlings may recruit in the shade of conspecific adults, but long-term recruitment under adults would have to occur without protection from herbivory, and without eventual release from shade.

The heavy browsing of seedlings in the open at Cachuma and Sedgwick Ranch and evidence that environmental stress (i.e., dried, brown foliage on seedlings) did not differ between seedlings in the open and seedlings under shrubs (Table 2) suggests that protection from herbivory may be the primary nurse plant effect there. Mortality estimates of the experimental seedlings, however, indicate that although herbivory was reduced by nurse shrubs, protection from environmental stress by shrubs was even more important in reducing mortality: more shoots dried in place than disappeared. It is possible that the relative importance of mortality due to herbivory versus environmental stress varied between the year when we measured natural seedling distributions and the years when we conducted the field experiment. Or it may have differed between the sites where we measured natural patterns of seedling distribution and the site where we conducted the experiment. Additionally, we may have overestimated mortality due to environmental stress because of undetected root herbivory and subsequent drying of shoots.

The fact that survivorship was inversely correlated (Fig. 4) with the number of seedlings that emerged under an individual shrub suggests that microhabitat differences were more important than seedling densities for determining seedling survival, at least in the early stages of development. This also emphasizes the importance of analyzing seedling survival by plots as well as by total seedlings. Microsite differences were not obvious in the field, but they were likely to include slight changes in elevation, slope aspect, soil characteristics or gopher densities. Bullock (1981) also reported similar patterns of high seedling survival in aggregated conditions for *Prunus ilicifolia* Walpers.

Reasons for different rates of oak seedling survival under different shrub species were not obvious either. High seedling survival may have been associated with species-specific characteristics of the nurse plants such as the amount of shade provided, root interactions, susceptibility to herbivory, or differences in throughfall chemistry. Differences in "nurse plant" quality among species have also been reported in desert communities (McAuliffe 1988).

Rainfall in central California was below average during each of the years of this study and it is unclear how facilitative effects might change in years with normal or above average rainfall. Although in wet years survivorship of seedlings may increase in open, unsheltered habitats, the fact that any seedlings at all survived two years of drought emphasizes the significance of the facilitative effects of nurse shrubs.

Natural oak/shrub nurse plant associations may be initiated by bird dispersal of acorns. Scrub Jays (*Aphelocoma coerulescens*) are potential dispersers of acorns into shrub protected sites (Griffin 1976). These birds have been observed burying acorns under shrubs in other California oak woodlands (Griffin pers. obs.). Individuals of this same species cache over 6000 acorns per bird per autumn in oak woodlands in Florida and recover only one-third of the these acorns (DeGange et al. 1989). Bird caching may also explain the clumped spatial distribution of naturally established seedlings.

Although nurse plant interactions have not been reported in oak woodlands, they are common in other semiarid and arid environments. Phillips (1909) and Everett et al. (1986) reported that *Pinus monophylla* Torrey & Fremont (single-leaved pinyon) required nurse plants to survive in parts of the Great Basin Desert. Nurse plant effects have also been reported for desert cacti (Steenbergh and Lowe 1969; Yeaton 1978; Nobel 1980; Franco and Nobel 1989), desert agave (Franco and Nobel 1988), desert shrubs (McAuliffe 1988), and desert trees (McAuliffe 1986). In these studies the effects of nurse plants on understory microclimate and herbivory were considered to be primary factors that improved the survivorship of seedlings.

Young plants may eventually compete with and kill, or outlive their nurse plants (McAuliffe 1984, 1988). This also may occur in *Q. agrifolia*-shrub interactions. We found young oaks that had grown through the tops of their nurse shrubs, and older oaks that had established in the shrubland which did not have living shrubs under their canopies, although shrubs surrounded the canopies of these same trees. It is conceivable that *Q. agrifolia* may eventually create an environment too low in light, moisture or nutrients for the survival or recruitment of shrubs. Thus a cycle of nurse plant facilitation and eventual tree-shrub competition may affect overall patterns and boundaries of shrubland, grassland, and woodland. In other areas that are similar to our study sites, *Q. agrifolia* appears to be successional to shrubs when fires are infrequent (Wells 1962; Griffin 1978; Davis et al. 1988).

Although our data indicate that shrubs significantly improve the survivorship of *Q. agrifolia* seedlings, two important questions remain. First, what proportion of this effect can be attributed to microsite differences? It is possible that oak seedlings and shrubs survive better in the same microsite and that the nurse plant phenomenon is simply an artifact. Second, what facilitative mechanisms are operating that improve seedling survival (e.g., seed deposition patterns, germination cues, shade, or herbivore refuge).

In conclusion, we have presented evidence that native shrubs can function as nurse plants for young *Q. agrifolia,* including associations between naturally occurring oak seedlings and chaparral shrubs and higher survival of planted seedlings under shrubs at a site where natural vegetation was being restored. The role of native shrubs as nurse plants may be important for the improvement of regeneration of *Q. agrifolia* as well as other oak species.

ACKNOWLEDGMENTS

We thank A. Ribbens and B. Shaw for assistance in the field, and officials at Cachuma State Park for access. Thoughtful reviews were provided by S. Bullock and L. D. Oyler. Partial funding and access to the experimental site was provided by Union Oil of California (UNOCAL).

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(Received 9 July 1990; revision accepted 4 Jan 1991.)

ANNOUNCEMENT

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The California Department of Fish and Game and the California Native Plant Society are publishing a book about California's endangered plants. The goal is to provide a readable and informative reference to help the general public understand the plight of endangered plants and their endangered habitats. The book will complete the two-volume set on California's threatened and endangered species. To date, the enthusiasm generated by "California's Wild Heritage, Threatened and Endangered Animals in the Golden State" has been tremendous and the public is interested in another volume. The companion volume on plants will be 150 pages and feature the over 200 California state-listed rare, threatened and endangered plants with excellent color photographs and illustrations. **We are searching for the best possible photographs of these species and their habitats.** A list of state-listed plants can be found in Smith and Berg's (1988) "CNPS's Inventory of Rare and Endangered Vascular Plants of California" or can be obtained from the Department of Fish and Game. Please send a list of color slides that you have of state-listed plants to: Diane Ikeda, Natural Heritage Division, California Department of Fish and Game, 1416 Ninth Street, Sacramento, CA 95814. For further inquiries, call (916) 327-5957.